

*Helicoradomenia juani* gen. et sp. nov., a Pacific  
Hydrothermal Vent Aplacophora  
(Mollusca: Neomeniomorpha)

by

AMÉLIE H. SCHELTEMA

Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, USA

AND

ALAN M. KUZIRIAN

Marine Biological Laboratory, Woods Hole, Massachusetts 02543, USA

**Abstract.** The aplacophoran *Helicoradomenia juani* gen. et sp. nov. is found in large numbers at the northeast Pacific vent sites of Juan de Fuca Ridge, Explorer Ridge, and Gorda Ridge. It is placed in the family Simrothiellidae on the basis of radular morphology (distichous bars with paired ventral pockets) and is separated from other genera in the family by the presence of solid epidermal spicules.

#### INTRODUCTION

Several closely related species of neomenioid (footed) Aplacophora occur at hydrothermal vents. They were originally assigned to the genus *Simrothiella* Pilsbry, 1878 (SCHELTEMA, 1988; TURNER, 1985, through personal communication from Scheltema), but re-examination of type material of *S. margaritacea* (Koren & Danielssen, 1877) indicates that the latter is generically distinct from the hydrothermal vent species on the basis of the radula alone (cf. Figure 2D, E). The type species for the new genus is described here.

#### MATERIALS AND METHODS

All specimens (365) were collected from the Endeavour segment of Juan de Fuca Ridge (47°57'N, 129°04-06'W, 2250 m), Explorer Ridge (49°46'N, 130°16'W, 1800 m), and Gorda Ridge (41°00'N, 127°30'W, 3271 m) from the deep submersible research vessels *ALVIN* and *PISCES*.

About 20 specimens were dissected or sectioned. Radulae, epidermal spicules, and copulatory spicules were dissociated from dissected anterior or posterior ends of specimens by dissolving tissue in hypochlorite solution (household bleach) or, for some radulae, in 10% NaOH solution. They were washed and placed in a drop of glycer-

ine for camera lucida drawing. After further washing, permanent slides were made of air-dried spicules and CMCP-10 (TURTOX)-mounted radulae. One specimen was prepared for histology by decalcifying the spicules with 0.5 M EGTA overnight, dehydrating in dimethoxy propane, and embedding in epon/araldite epoxy resin. Sections were cut at 1.5  $\mu$ m and stained with Richardson's stain (azure II and methylene blue). Standard paraffin sections (7  $\mu$ m) were also cut and stained with Mallory-Heidenhain trichrome. Types are deposited in the National Museum of Natural History (NMNH), Washington, DC.

**Terminology:** *Skeletal* (=tangential) spicules are those that lie within the cuticle and spiral around the body at a 45° angle, crossing each other at 90°; *upright* (=radial) spicules extend out of the cuticle; *isochromes* are boundaries between color bands produced in solid spicules by cross-polarized light; *distichous* refers to a radula formed by repeated rows of two teeth each (formula: number of rows  $\times$  1·1); *denticulate bar* is a bar-like radular tooth with denticles on the side opposite to the attachment of the tooth to the radular membrane; *vestibule* (=atrium) is the anterior cavity that lies above the mouth either united with or separate from the mouth opening and that contains sensory papillae; *oral cavity* (=buccal cavity) is the ventral space into which the mouth opens and which leads dorsally to the *pharynx*.

## SYSTEMATICS

Subclass Neomeniomorpha Pelseneer, 1906

Ventroplicida Boettger, 1956

Solenogastres Gegenbaur, 1878 (*partim*), Salvini-Plawen, 1967

Aplacophoran mollusks with a narrow foot in a ventral furrow, an anterodorsal vestibule with sensory papillae, a combined stomach-midgut gland, serial lateroventral muscles, a mantle cavity without ctenidia, and paired hermaphroditic gonads.

## Family SIMROTHIELLIDAE

Salvini-Plawen, 1978

**Type species:** *Solenopus margaritaceus* Koren & Danielsen, 1877.

Radula with distichous denticulate bars and short or long paired anteroventral radular pockets; spicules hollow or solid; skeletal spicules present or absent; morphology of ventral salivary glands varied.

*Helicoradomenia* Scheltema & Kuzirian,  
gen. nov.

Plump to somewhat elongate, nearly smooth to spiny, 5 mm or less in length, dorso-posterior sense organ and sometimes dorso-frontal sensory pit present; proboscis large, protrusible; mouth at proximal end of vestibule; pedal pit large, often protruded; cuticle thin, epidermal glands not stalked; spicules solid, upright, skeletal spicules lacking; radula large, lateral denticles longest; radula spiraling into paired anteroventral radular pockets, first-formed teeth not retained; paired ventral salivary glands small, opening through paired ducts; paired sac-like seminal receptacles; single gametopore; copulatory spicule pockets paired, 2 or more long spicules per pocket; mantle cavity with long respiratory papillae.

**Range:** Eastern and western Pacific hydrothermal vents.

**Etymology:** *helico* = helical, *rad* = abbreviation for radula, *menia* = moon, usual ending for neomenioid ("new moon") aplacophorans.

*Helicoradomenia juani* Scheltema & Kuzirian,  
sp. nov.

(Figures 1–5)

**Holotype:** 3.4 mm long, anterior diameter 0.7 mm, mid-body 1.0 mm, posterior 1.6 mm. Endeavour Segment, Juan de Fuca Ridge, 47°57'N, 129°04'W, 2250 m (DSRV *ALVIN* Dive 1419). NMNH No. 836328.

**Figured paratypes:** Nos. 1, 3, 6, 9, 14, from type locality. NMNH Nos. 860188, 860187, 860191, 860189, and 860190, respectively.

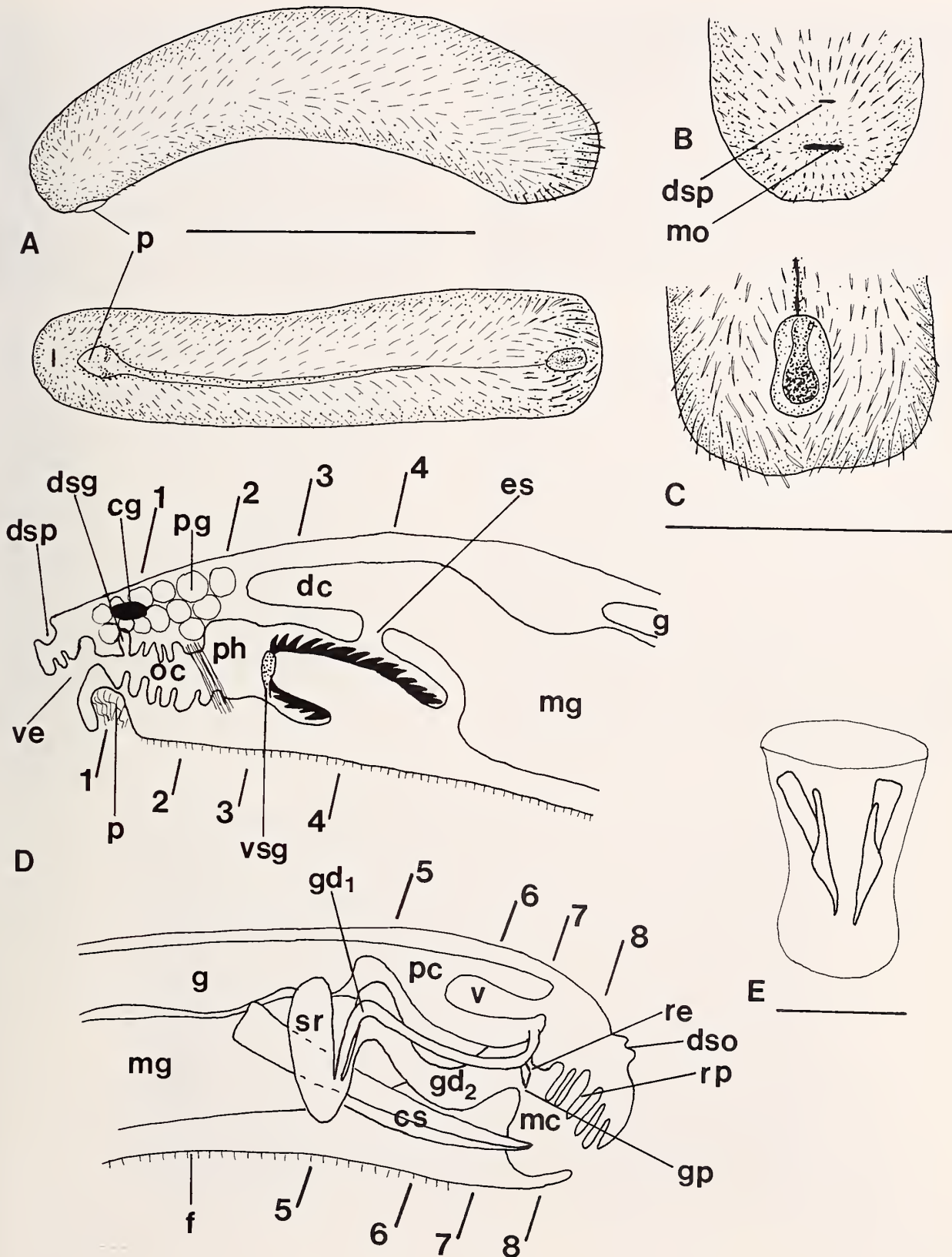
**Distribution:** Explorer, Juan de Fuca, and Gorda ridges, 1800–3271 m.

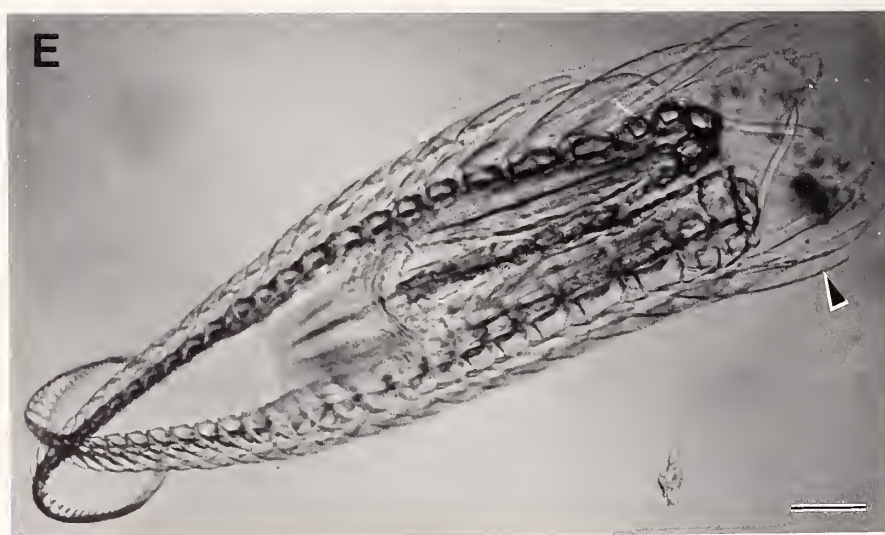
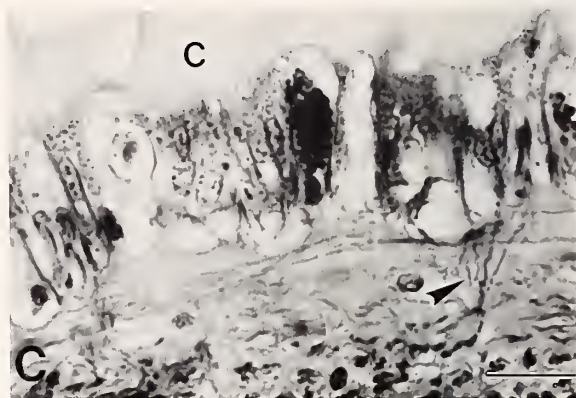
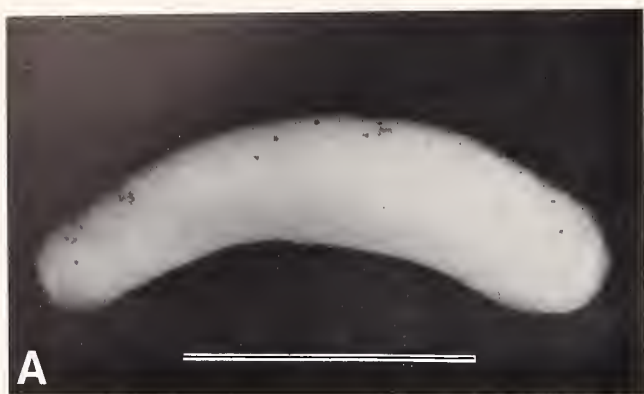
**Diagnosis:** Appearance fuzzy, length to 5 mm, narrowest anteriorly, mean index (length : diameter) at midbody 4:1; with dorso-frontal sensory pit; spicules widest at base and distally pointed, varying from short, wide, and recurved (110  $\mu$ m long, 18  $\mu$ m wide, 10  $\mu$ m thick) to long, slender and curved (200  $\mu$ m long, 14  $\mu$ m wide, more than 10  $\mu$ m thick); radular formula 34–35  $\times$  1.1, teeth with 5 or 6 denticles, lateral denticle twice length of next adjacent one; 2 spicules per copulatory spicule pocket, curved, sharply pointed distally, up to 1 mm long, shorter spicule of pair with proximal process; accessory copulatory spicules 2 on each side, with 3 low bumps.

**External anatomy and hard parts:** Body (Figures 1A–C, 2A) somewhat elongate, index at midbody 3–4:1; anterior end rounded; wider posterior end slightly pointed with flattened ventral region around mantle cavity opening; mouth slit lateral; dorso-frontal sensory pit obvious as lateral slit; dorso-terminal sense organ not evident externally; mantle cavity opening axial, oval. Epidermal spicules (Figure 3A, B) of 5 types, longest at posterior end of body, usually thickest near base: (1) evenly curved, narrow, width even except tapered distally to point, up to 130  $\mu$ m long  $\times$  11  $\mu$ m wide, 7  $\mu$ m to more than 10  $\mu$ m thick, grades into (2) straight or evenly curved, width even except expanded basally and tapered distally to blunt point, up to 200  $\mu$ m long  $\times$  15  $\mu$ m wide, more than 10  $\mu$ m thick; (3) broad, base recurved proximal to indentation or unevenly curved, distally tapered to point, up to 112  $\mu$ m long  $\times$  18

Figure 1

*Helicoradomenia juani* gen. et sp. nov. A: Holotype, showing spicule orientation and somewhat protruded pedal pit, lateral (above) and ventral views. B: Holotype, anterior end, frontal view showing relationship of dorso-frontal sensory pit and opening to mouth and vestibule. C: Holotype, posterior end, ventral view, with oval-shaped mantle cavity opening. D: Schematic sagittal sections of anterior (above) and posterior ends; transverse sections 1–8 are keyed to histologic sections in Figures 4 and 5. E: Copulatory spicules *in situ*, paratype no. 3, ventral view of posterior end (rotated 90° from D, mantle opening below), tissue partially dissolved. Key: cg, cerebral ganglion; cs, copulatory spicule; dc, dorsal cecum; dsg, dorsal salivary gland; dso, dorso-terminal sense organ; dsp, dorso-frontal sensory pit; es, esophagus; f, foot; g, gonad; gd<sub>1,2</sub>, upper and lower gametoducts; gp, gametopore; mc, mantle cavity; mg, midgut (stomach-intestine); mo, opening to vestibule and mouth; oc, oral cavity; p, pedal pit; pc, pericardial cavity; pg, pedal gland; ph, pharynx; re, rectum; rp, respiratory papilla; sr, seminal receptacle; v, ventricle; ve, vestibule; vsg, ventral salivary gland. Scale bars: A = 2.0 mm, B, C = 1.0 mm, E = 0.05 mm.





$\mu\text{m}$  wide, 9  $\mu\text{m}$  or less thick; (4) short, straight, rounded basally, tapered distally to point, up to 74  $\mu\text{m}$  long  $\times$  15  $\mu\text{m}$  wide, 7  $\mu\text{m}$  or less thick; (5) short, straight or curved, distally pointed, base straight, up to 80  $\mu\text{m}$  long  $\times$  11  $\mu\text{m}$  wide, 9  $\mu\text{m}$  or less thick. Pedal-groove spicules short and broad, up to 70  $\mu\text{m}$  long  $\times$  16  $\mu\text{m}$  wide, 4–5  $\mu\text{m}$  thick.

Copulatory spicules (Figures 1D, E, 3D, E, 5C) 2 per pocket, curved dorsally, sharply pointed distally, longer spicule up to 1 mm in length with straight base, shorter spicule with proximal process, medioventral to and partially wrapped around longer spicule. Paired accessory spicules (Figures 3C, 5G) 2 on each side, recurved, each with 3 low bumps on base.

Radula (Figures 2B, D, 3F, G) with single turn into ventral pockets; 34 or 35 rows; teeth with 5 or 6 denticles, lateralmost denticle twice length of next adjacent denticle; bar about 115  $\times$  12  $\mu\text{m}$ , lateral denticle 30  $\mu\text{m}$ ; dimensions of older teeth smaller.

**Internal anatomy (Figure 1D):** Cuticle 22  $\mu\text{m}$  thick. Epidermis (Figure 2C) 22  $\mu\text{m}$  thick, with more than one type of secretory cell, pierced by tubules from hemocoel. Body-wall musculature well developed. Pedal pit lined by large secretory cells (Figure 4A). Vestibule with few low, broad papillae; cirri grouped at mouth opening with which vestibule is united. Oral cavity deeply folded, also with cirri (Figure 4A). Multicellular dorsal salivary gland small (Figure 4A). Pharyngeal wall smooth (Figure 4B). Ventral salivary glands paired, small, tube-shaped, multicellular, unbranched, non-basophilic staining (Orange G), each opening through separate duct into anterior end of anteroventral radular pocket (Figure 4C). Anteroventral radular pocket as paired pouches which remain connected medially for some distance (Figure 4C). Radula bolsters large, bolster muscles well developed (Figure 4D). Short esophagus present (Figure 4D). With single, short dorsal midgut cecum (Figure 4D); midgut sacculate. Pericardial cavity large (Figure 5C); heart large, free within pericardium, opening from a posterior dorsal sinus (Figure 5C, D). Seminal receptacles as paired, large tubes lying in a dorsoanterior to ventroposterior position, each opening through a narrow tube leading dorsally to lower gametoduct (Figure 5A, B). Upper gametoduct opens into sem-

inal receptacle through a narrow duct adjacent to the tube joining the seminal receptacle and lower gametoduct (Figure 5B). Gametopore single, opening into mantle cavity below rectum (Figure 5E). Mantle cavity with numerous long respiratory papillae (Figure 5F). Dorsoterminal sense organ large, papillate, seen only in sectioned material.

**Remarks:** The reproductive system of these animals is unusual because (1) the upper gametoduct is joined to the distal end of the seminal receptacle rather than to the lower gametoduct, and (2) the position of the tubes connecting the seminal receptacles to upper and lower gametoducts is asymmetrical, being medial to the copulatory spicules on the left side and lateral to them on the right side in the specimen sectioned (Figure 5A, B).

The ventral salivary glands are embedded in the muscles of the radula (Figure 4C). They are unusually small and do not have a basophilic reaction to trichrome staining. This condition is atypical from the strong basophilia found in the salivary glands of most other neomenioids and presumably reflects diet. Nematocysts were not found in the midgut of *Helicoradomenia juani*, and Cnidaria did not occur where this species was collected. It is thus assumed that *H. juani* is not a cnidarivore as are most neomenioids. The organic matter seen in the gut has not been identified.

**Relationships:** Isolated radulae have been examined from three genera belonging to the family Simrothiellidae Salvini-Plawen: *Simrothiella* Pilsbry, 1898 (Figure 2E), *Kruppomenia* Nierstrasz, 1903a (synonymy with *Simrothiella*, SALVINI-PLAWEN, 1978, in error), and a new genus to be published which will include "*Simrothiella*" *schizoradulata* Salvini-Plawen, 1978. All have distichous bars and short to very long paired anteroventral radular pockets. It is this radular morphology that is the basis for placing *Helicoradomenia* in the Simrothiellidae. The epidermal spicules provide a basis for generic separation. In *Helicoradomenia* they are solid and thus differ from the hollow spicules found in all other genera in the family, which also includes *Cyclomenia* Nierstrasz, 1902, *Uncimienia* Nierstrasz, 1903b, *Birasoherpia* Salvini-Plawen, 1978, *Biseramenia* Salvini-Plawen, 1968, and *Sialoherpia* Salvini-Plawen, 1978. Although the illustrated radulae of these

Figure 2

A–D. *Helicoradomenia juani*. A: Holotype, anterior to left (cf. Figure 1A). B: Scanning electron photomicrograph of part of left half of radula from above, medial edge to left, paratype no. 6; five rows of teeth, some with five and some with six denticles, shown. Arrowhead indicates longest, most lateral denticle. C: Light micrograph of histologic section of epidermis and cuticle (c) of mantle showing various gland cells and innervation by nerve fibers (arrowhead). D: Light micrograph of entire radula from below showing helical position of teeth from anteroventral radular pocket, paratype no. 14; newest tooth indicated by arrowhead. E. Light micrograph of radula of *Simrothiella margaritacea* (Koren & Danielssen, 1877), ventral view with elongated paired ventral radular pockets to left and long lateral teeth (arrowhead) extending into pharynx on right (R. V. Chain 106 Stn 316, 50°58.7'N, 13°01.6'W, 2173 m). Species determination from comparison with radula isolated from a syntype, Bergen Museum no. 2078. Scale bars: A = 2.0 mm; B, C = 0.02 mm; D, E = 0.1 mm.

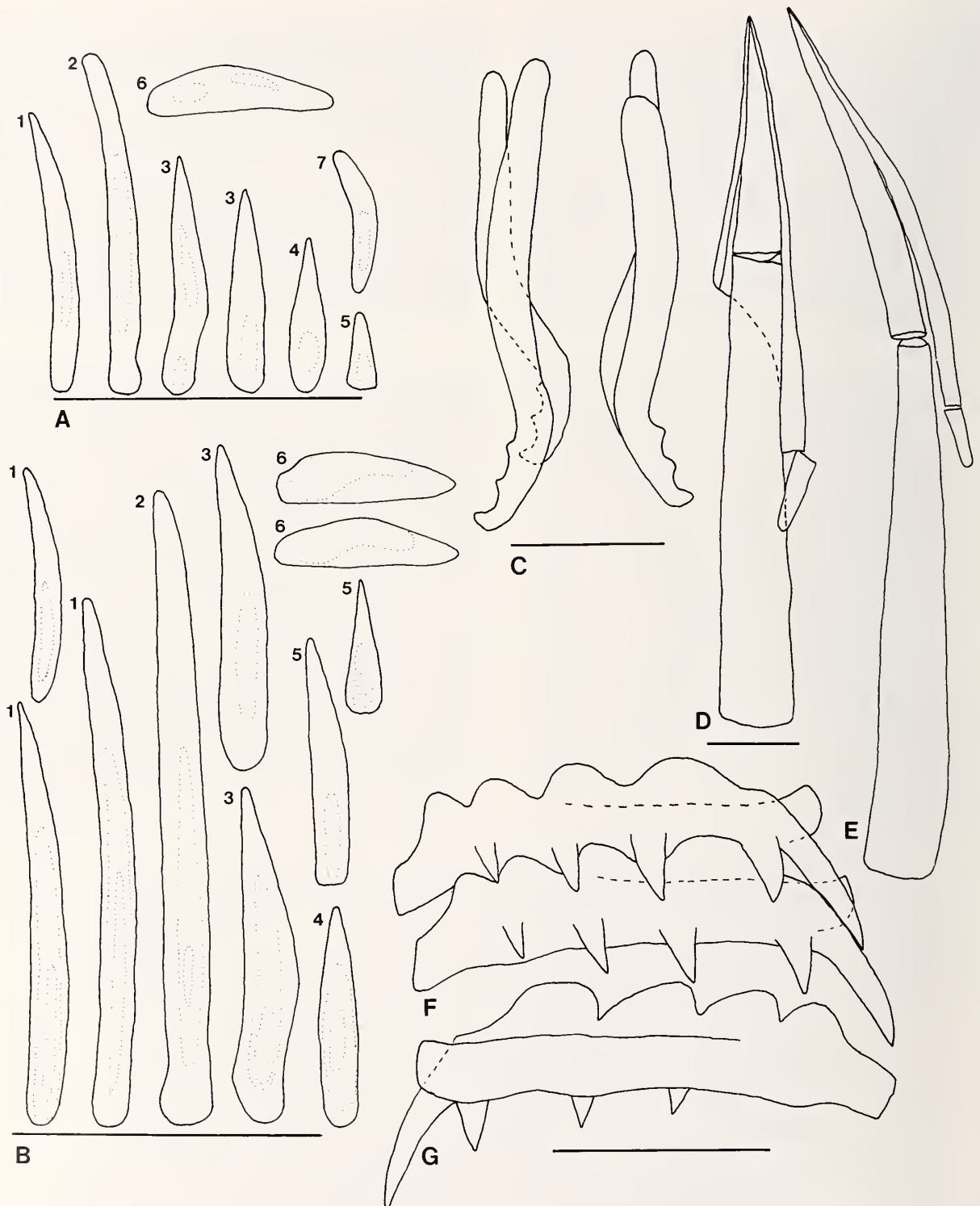


Figure 3

*Helicoradomenia juani*, hard part morphology. A, B: Epidermal spicules, anterior and posterior, respectively, paratype no. 1; selected isochromes indicated by dotted lines; 1-5, see text; 6, pedal-groove spicules; 7, oral spicule. C: Accessory copulatory spicules, paratype no. 1 (cf. Figure 5G). D, E: Copulatory spicules from paratype nos. 1 and 9, respectively. F: Two adjacent teeth from right side of radula, paratype no. 1. G: Single radular tooth, right side, paratype no. 1, view from beneath radular membrane showing bar. Scale bars: A, B, D, E = 0.1 mm; C, F, G = 0.05 mm.

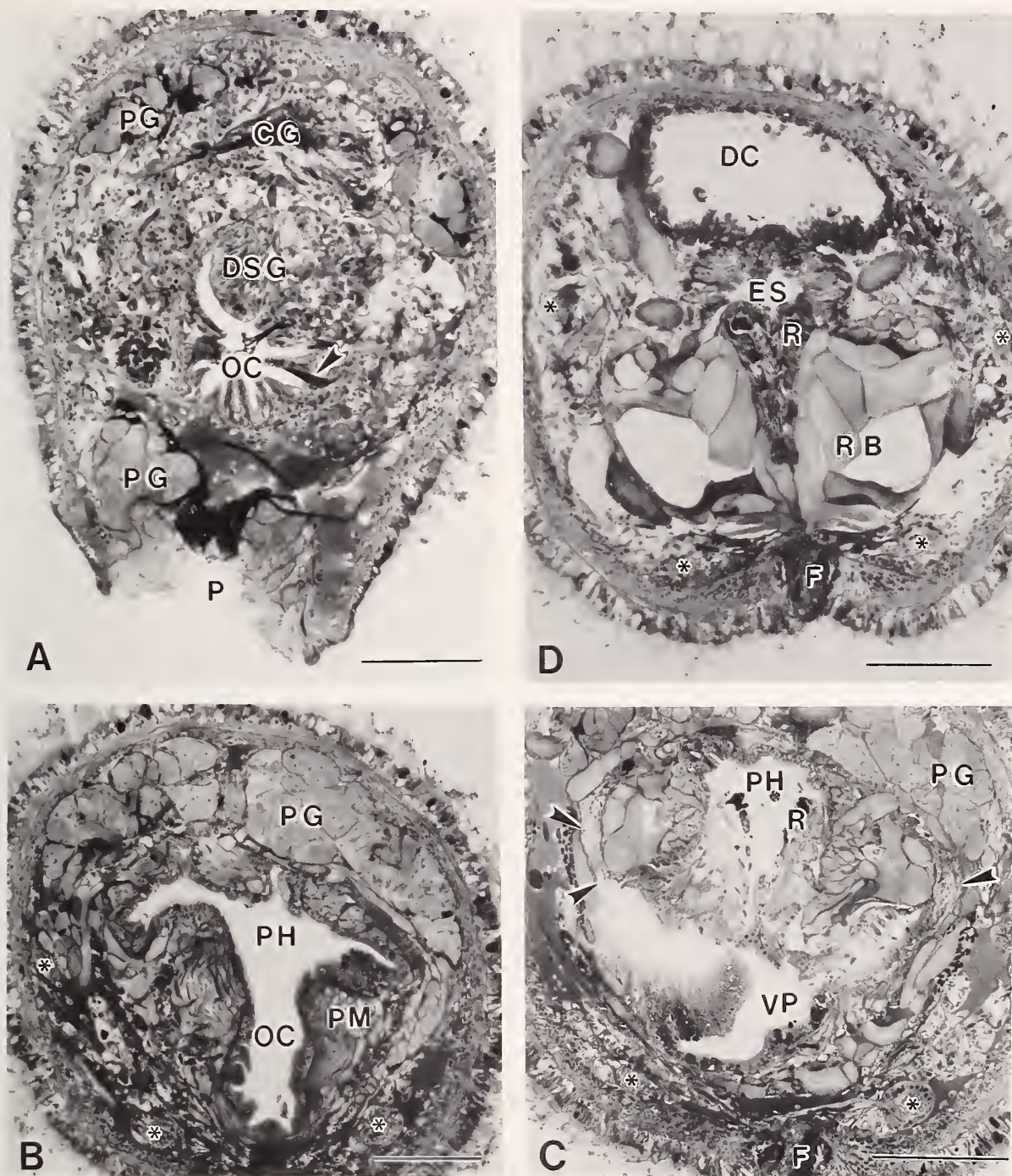
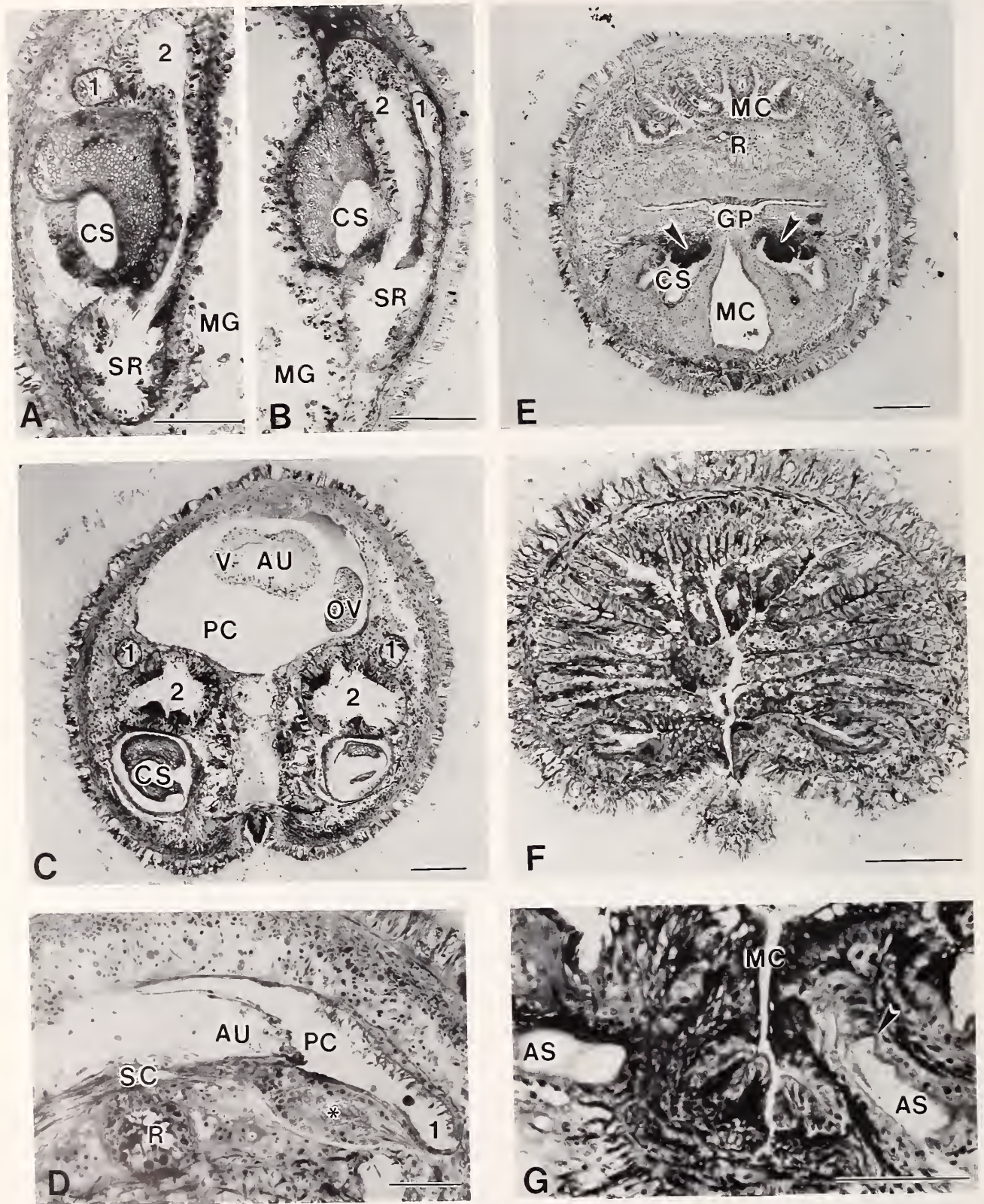


Figure 4

Anterior end, *Helicoradomenia juani*, transverse histologic sections 1 through 4 of Figure 1D. A: Section 1 through cerebral ganglion, dorsal salivary gland, oral cavity with cirri (arrowhead), and pedal pit. B: Section 2 through oral cavity, pharynx, and pharyngeal muscles. C: Section 3 through paired ventral salivary glands (arrowheads), gland on left shown opening into anteroventral radular pocket. D: Section 4 through dorsal cecum of midgut, esophagus, radula and radula bolster with well-developed musculature and large chondroid-like cells. Key: CG, cerebral ganglion; DC, dorsal cecum; DSG, dorsal salivary gland; ES, esophagus; F, foot; OC, oral cavity; P, pedal pit; PG, pedal gland; PH, pharynx; PM, pharyngeal muscle; R, radula; RB, radula bolster; VP, anteroventral radular pocket. Asterisks indicate ganglia of lateral and anteroventral nerve cords. Scale bars: A-D = 0.1 mm.





latter five genera are drawn from sectioned material only, they all appear to be distichous denticulate bars.

SALVINI-PLAWEN (1978) placed the family Simrothiellidae in the order Cavibelonia, a grouping based on possession of hollow spicules. *Helicoradomenia* is the second genus with solid spicules to be placed in a cavibelonid family. The genera of Pararrhopalidae, if brought together on the basis of possessing fishhook-shaped spicules, also form a cavibelonid family with both solid (*Ocheyoherpia*) and hollow spicules (SCHELTEMA, in press). The families of Cavibelonia vary in respect to type of radula and ventral salivary glands and in presence or absence of skeletal spicules (SALVINI-PLAWEN, 1985). The morphologies of these structures are not unique to the Cavibelonia but are found in other orders as well. We therefore conclude that the order Cavibelonia is polyphyletic and needs to be revised. The family Simrothiellidae should probably be raised to ordinal level, but not until further comparisons of newly collected material have been made.

**Distribution:** Several vent species of *Helicoradomenia* still to be described occur at other rift sites in the eastern Pacific other than those off the northwest United States where *H. juani* is found: off the Galápagos (2 species), at 13°N (1 species), at 20°N (3 species, one in common with Galápagos), and from Gorda Ridge (1 species). The genus has also been collected from western Pacific rift sites in the Marianas Back Arc and Lau basins. None of these species has been collected in such high numbers as *H. juani*.

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Figure 5

Posterior end, *Helicoradomenia juani*, transverse histologic sections 5 through 8 of Figure 1D. A, B: Section 5, left and right sides, respectively, showing the connections between the upper and lower gametoducts and the paired seminal receptacles; position of ducts on left side lies between copulatory spicules and midgut, whereas those on right lie lateral to the copulatory spicules. C: Section 6 through pericardium with ovum, heart, upper and lower gametoducts, and copulatory spicule pockets. D: Section 7 through posterior end of pericardial cavity where it connects to upper gametoduct, beginning of auricle, rectum and suprarectal commissure arising from large ganglion of the lateral nerve cord (asterisk). E: Unnumbered section between sections 7 and 8 through proximal end of mantle cavity just anterior to openings of rectum and gametopore and through the copulatory spicule glands (arrowheads). F: Section 8 through mantle cavity with long respiratory papillae. G: Unnumbered section posterior to F through the accessory copulatory spicules (dissolved) of the mantle, bump indicated by arrowhead (cf. Figure 3C). Key: 1, upper gametoduct; 2, lower gametoduct; AS, accessory copulatory spicule; AU, auricle; CS, copulatory spicule/spicule pocket; GP, gametopore; MC, mantle cavity; MG, midgut gland; OV, ovum; PC, pericardial cavity; R, rectum; SC, suprarectal commissure; SR, seminal receptacle; V, ventricle. Scale bars: A-C, E, F = 0.1 mm; D, G = 0.05 mm.